Mar Biol (2008) 155:211–221
DOI 10.1007/s00227-008-1019-7

ORIGINAL PAPER

Photosynthetic performance of giant clams, *Tridacna maxima* and *T. squamosa*, Red Sea

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Received: 19 December 2007 / Accepted: 12 June 2008 / Published online: 8 July 2008

Abstract Two species of giant clams, *Tridacna maxima* and *T. squamosa*, coexist in the Red Sea, but exhibit distinctly different depth distributions: *T. maxima* mostly occurs in shallow waters (reef flat and edge), while *T. squamosa* may occur down to the lower fore-reef slope. Giant clams have been described as mixotrophic, capable of both filter-feeding and photosynthesis due to algal symbionts (zooxanthellae), therefore, observed depth preferences were investigated in relation to possible differences in autotrophy vs. heterotrophy. This study was conducted from April to June 2004, at the reef near the Marine Science Station, Aqaba, Gulf of Aqaba, Red Sea, and in May 2007, at a reef near Dahab, Sinai Peninsula, Egypt. In situ measurements using a submersible pulse amplitude modulated fluorometer (Diving PAM), revealed no significant differences in effective PSII quantum yield ($\Delta F/Fm'$) and relative electron transport rates (ETR) between the two species; but rapid light curves (ETR vs. light, photosynthetically active irradiance, PAR) showed significant differences in maximum photosynthetic rates (ETR_{max}), with 20% higher values in *T. maxima*. Chamber incubations displayed higher net and gross oxygen production by *T. maxima* (88.0 and 120.3 μmol O_2 cm^{-2} mantle area day^{-1}) than *T. squamosa* (56.7 and 84.8 μmol O_2 cm^{-2} mantle area day^{-1}); even under shading conditions (simulated depth of 20 m) *T. maxima* still achieved 93% of the surface gross O_2 production, whereas *T. squamosa* reached only 44%. A correlation was found between ETR and net photosynthesis measured as oxygen production (*T. maxima*: $R^2 = 0.53$; *T. squamosa*: $R^2 = 0.61$). Calculated compensation depth (CD) (gross photosynthesis equals respiration) in *T. maxima* (16 m) matches the maximum depth of occurrence in this study (17 m). By contrast, the CD of *T. squamosa* (9 m) was much shallower than the maximum vertical range (42 m). Findings suggest *T. maxima* is a strict functional photoautotroph limited by light, whereas *T. squamosa* is a mixotroph whose photoautotrophic range is extended by heterotrophy.

Communicated by J.P. Grassle.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-008-1019-7) contains supplementary material, which is available to authorized users.

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Introduction

Like many other reef organisms, including corals, giant clams (Tridacnidae) live in symbiosis with dinoflagellates

(Jeffrey and Haxo 1967; Baillie et al. 1998; Belda-Baillie et al. 1999). The photosynthates of these zooxanthellae cover a major part of the clam's energy demand (Trench et al. 1981; Klumpp et al. 1992; Hawkins and Klumpp 1995). This symbiosis, coupled with the efficient recycling of nutrients, is a vital adaptation to life in oligotrophic waters (Muscatine and Porter 1977; Trench 1979; Belda et al. 1993; Hawkins and Klumpp 1995) and is responsible for the exceptionally high growth rates of the Tridacnidae among bivalves (e.g. Klumpp and Griffiths 1994). In shallow waters, the zooxanthellae have been shown to fully cover the respiratory carbon demand of the clams (*Tridacna maxima*, Trench et al. 1981; *T. gigas*, Klumpp et al. 1992; *T. tevoroa* and *T. derasa*, Klumpp and Lucas 1994) by providing their host with photosynthetic products such as glucose and amino acids (Streamer et al. 1988).

Two species of giant clams, *T. maxima* and *T. squamosa,* co-exist in the Gulf of Aqaba, Northern Red Sea. They exhibit different depth distributions: *T. maxima* is concentrated around the reef flat and reef edge, scarcely deeper than 10 m (maximum 17 m, this study), whereas *T. squamosa* is found over the entire depth range, from the reef flat to the lower fore-reef slope down to 42 m (this study). A similar depth segregation has been observed between the shallow-dwelling *T. derasa* and the deep-dwelling *T. tevoroa* in Tonga, and attributed to differential photosynthetic adaptations of 'giant clams' to light (Klumpp and Lucas 1994). It is unresolved, however, if autotrophy alone accounts for the observed vertical distribution patterns in giant clams between high-light and low-light adapted species, or, if the degree of heterotrophy, i.e. the capacity to exploit organic matter (e.g. planktonic food), is a more important factor allowing certain clams to extend their range of distribution to reef regions beyond their compensation depth (CD) (where gross photosynthesis equals respiration).

The present study addressed the photosynthetic performance of *T. maxima* and *T. squamosa* in response to diurnal and vertical variations in light availability. Although the advent of diver-operated pulse amplified modulated underwater fluorometry (Diving PAM) allows measurement of the photosynthetic activity of symbiotic corals and anemones in situ (e.g. Beer et al. 1998; Ralph et al. 1999; Warner et al. 2002), data on giant clams is scarce (one individual of *T. maxima*: Ralph et al. 1999), owing to difficulties in obtaining standardized replicate measurements on the notoriously fickle mantle. The present study combined Diving PAM measurements in the field and in the laboratory with chamber incubation experiments, in order to determine primary productivity and respiration, and to reveal the extent to which both species rely on autotrophic input and how this may explain their different depth distributions.

Materials and methods

Study site

Giant clams were investigated both in situ, at the Marine Reserve of the Aqaba Marine Science Station (MSS), Jordan (Gulf of Aqaba, Red Sea; N 29°27′31″, E 34°58′32″), and in the MSS' mariculture facilities, from April to June 2004. Large adult specimens naturally occurring in the reef (not transplanted), were also measured in situ near Dahab, Egypt, approximately 120 km further south in the Gulf of Aqaba, in May 2007.

Investigated clams

Chamber incubations were carried out for medium-sized specimens (shell length, SL, 11–12 cm for both species) maintained in the MSS aquaculture facilities, i.e. ~ 1 m depth. Details on the maintenance conditions of these clams are described by Roa-Quiaoit et al. (2004). Fluorescence measurements accompanying the chamber incubation were carried out on the same individuals. Photosynthesis (electron transport rates, ETR vs. light, photosynthetically active irradiance, PAR) measurements, i.e. rapid light curves (RLC), were conducted with adult clams (SL > 15 cm) also maintained in outdoor tanks. Investigations in the field were carried out on naturally occurring adult clams (SL > 15 cm) on a reef near Dahab, Egypt.

Fluorescence measurements

All fluorescence measurements were obtained with an underwater pulse amplified modulated fluorometer, the 'Diving-PAM' (Heinz Walz Ltd.). A 'stripped-down' version of the 'Universal Sample Holder DIVING-USH' was used to access the mantle at a standardized distance of 1 cm, without touching the sensitive tissue (the sample holder contains the leaf clip and attaches the fibre optic as well as the light sensor). Two types of measurements were performed: (1) measurements under natural light conditions, providing data on photosynthetic effectiveness (effective PSII quantum yield, $\Delta F/Fm'$) and the ETR, as a quantitative (here relative) measure of photosynthesis, always accompanied with simultaneous light measurements made with the light sensor of the Diving PAM; (2) induced 'RLC', i.e. photosynthesis vs. irradiance ($n = 3$–5 individual^{-1}), using consecutive flashes of artificial ('actinic') light, of increasing intensity. The effective PSII quantum yield ($\Delta F/Fm'$) is a dimensionless value given by the equation: $(Fm' - F)/Fm'$); where Fm' is the maximum yield (in the given light state), and F the steady state fluorescence yield (in this particular state), monitored

briefly before the saturation pulse (Ralph et al. 1999). The ETR (in µmol quanta m^{-2} s^{-1}) is given by: ETR = $\Delta F/Fm' \times PAR \times 0.5 \times$ ETR-factor; where PAR is the photosynthetically active radiation (in µmol quanta m^{-2} s^{-1}); the ETR-factor is the assumed light absorbance of the sample, the clam tissue, i.e. the proportion of light not lost due to reflection or by shining through the sample. As the ETR-factor is unknown for giant clams, it was set to unity; thus the ETR presented is a relative rate, not an absolute one (relative ETR); 0.5 represents the assumed equal distribution of electrons between the two photosystems. $\Delta F/Fm'$ and ETR values are reported as averages (± standard error, SE) of 3–10 (medium-sized specimens) and 6–15 (large/adult specimens) measurements individual^{-1} carried out at random over the mantle surface.

Comparative investigations were always conducted under comparable light conditions (e.g. equal depth and time of the day) to provide a common basis for $\Delta F/Fm'$ and ETR. The technical details and measuring principles of the Diving-PAM are provided by Schreiber (1986) and are also available at http://www.walz.com/support/downloads/downloads/pdfs/diving3ea.pdf

A depth profile of $\Delta F/Fm'$ of wild stock giant clams were obtained in Dahab in May 2007, where *T. maxima* ($n = 29$) was investigated down to 17 m (the deepest depth for this species found during this study) and *T. squamosa* ($n = 16$) down to 33 m. Measurements from different days were assembled to produce the depth profile. Ambient light intensities recorded by the internal light sensor of the Diving PAM were logged simultaneously with each $\Delta F/Fm'$ measurement.

To simulate the metabolic performance of *T. maxima* and *T. squamosa* in shallow and deep waters respectively, netting was used to reduce light levels to 468 ± 104 (mean ± SE) µmol quanta m^{-2} s^{-1}, corresponding to 3 m water depth, and 128 ± 59 (mean ± SE) µmol quanta m^{-2} s^{-1}, corresponding to ~ 20 m water depth, according to the light vs. depth relationship established by this study (an additional PAR depth profile, obtained at one time, $n = 21$, consisting of 5–14 single measurements per depth; $PAR = -188.57\ (1 - e^{-695.35\ (x)})$, $R^2 = 0.957$, Supplementary data, Fig. 1). Individuals were allowed to adapt to shading, i.e. low light conditions, for 10 days prior to the incubations and PAM measurements. Fluorescence measurements were taken before and after each short-term incubation on three or four replicate specimens of both *T. maxima* and *T. squamosa*.

Diel variations in photosynthetic performance were measured over a single day for each species (during sunlight: 12.2 h, on 19 and 22 June 2004) with hourly incubations during sunny weather typical for the study area. Fluorescence measurements were taken before and after each of the incubations.

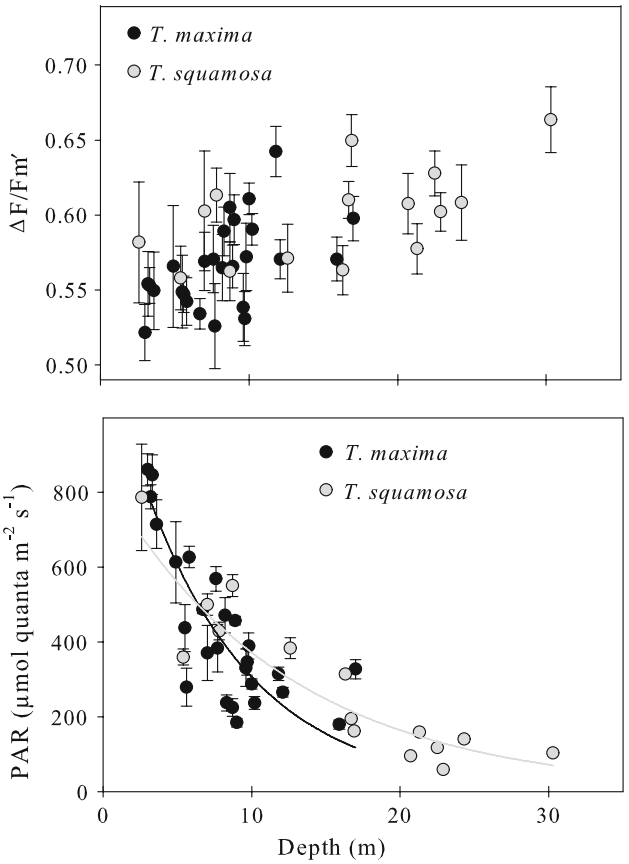

Fig. 1 *Tridacna maxima* and *T. squamosa*. **a** depth profile of naturally occurring giant clams and their effective PSII quantum yield ($\Delta F/Fm'$), Dahab, Egypt; linear increase of $\Delta F/Fm'$ with depth, **b** light intensities recorded concomitant with the depth profile of $\Delta F/Fm'$, photosynthetically active radiation (*PAR*, µmol quanta m^{-2} s^{-1}) with depth (m), *T. maxima*: $R^2 = 0.56$ and $y = 1197\ e^{-0.136x}$; *T. squamosa*: $R^2 = 0.64$ and $y = 843\ e^{-0.082x}$, *T. maxima* $n = 29$ and *T. squamosa* $n = 16$, mean ± SE

Rapid light curves were conducted with *T. maxima* ($n = 3$) and *T. squamosa* ($n = 3$), using standard Diving-PAM settings 4 through 12 (out of 1–12 steps, the Diving-PAM applies eight steps per light curve + an initial value for *F*, which is recorded before sending the actinic light pulses), corresponding to 120, 293, 394, 518, 691, 1,175, 1,628, 2,342, and 3,889 quanta m^{-2} s^{-1} (PAR), as determined by calibration with the PAM light sensor. This is equivalent to approximately 10 to 400% of maximum ambient light intensities at noon (~ 1,000 PAR µmol quanta m^{-2} s^{-1}) in shallow water (~ 0.5 m).

Chamber incubations

Chamber experiments were conducted in a water bath in the MSS outdoor raceways, with near-ambient flow velocities of 10–15 cm s^{-1} and near-ambient water temperatures (< 1°C difference) as determined by HOBO

temperature loggers (Onset). Prior to the experiments, clam shells were thoroughly brushed to remove fouling organisms. Incubations took place in cylindrical, transparent incubation chambers (volume: 10 l, details in Wild et al. 2004) for determination of net photosynthesis (P_n) from oxygen concentration increases, according to $P_n = [O2 (t_1)] - [O2 (t_0)]$, in time series or at the beginning and end of each incubation. The same clams were also incubated in opaque PVC-foil wrapped chambers to measure bulk respiration rates (R) from oxygen concentration decreases over the incubation time. Gross photosynthesis (P_g) was calculated as $P_g = P_n + R$. O_2-concentrations were determined using Winkler titration (Winkler 1888) and normalized to chamber volume. Clam-free controls (light and dark) showed no detectable O_2-differences attributable to plankton metabolism in the water ($n = 4$, two-sided t-test, heterogeneity of variance, $P = 0.8$). All chamber incubations were accompanied with fluorescence measurements before and after each incubation (fluorescence measurements as described above), with concomitant light measurements using the light sensor of the Diving PAM.

Short-term incubations were used to investigate the clams' metabolic performance under shallow (high light, 3 m) and simulated deep (low light, 20 m) water, using netting to reduce light levels (468 ± 104 µmol quanta m^{-2} s^{-1} and 128 ± 59 µmol quanta m^{-2} s^{-1}, see also fluorescence measurements above). Individuals were allowed to adapt to shading, i.e. low light, conditions for 10 days prior to the incubations and PAM measurements. These short-term incubations (2 h) were carried out with three or four replicate specimens for both *T. maxima* and *T. squamosa*. Respiration rates were not significantly different between species or illumination levels (two-tailed U-tests, $P = 0.95$).

Diel variations in photosynthetic performance were measured during one day, for each species (in sunlight, 12.2 h, 19 and 22 June 2004, following the course of a day with hourly incubations.

Standardization of metabolic rates in giant clams is conceptually difficult as the bulk of the photosynthetic algae occurs within the upper 5 mm of the mantle (Ishikura et al. 1997); so that photosynthesis may vary in proportion to mantle area. Respiration, by contrast, applies to the entire holobiont (i.e. the clam and the zooxanthellae) and thus varies with mass rather than area, where mass is again proportional to SL (Klumpp and Griffiths 1994, for dry tissue mass and SL, $DM = a \times SL^b$ for four species of giant clams, including *T. squamosa*, $R^2 \geq 0.94$ with $b = 3.2$–3.5). Thus, as the clams grow they increase disproportionally in biomass (cube of the SL) relative to photosynthetically active mantle area (square of the SL).

An SL-to-mantle area relationship was established for *T. squamosa* ($n = 11$) and *T. maxima* ($n = 18$) of various sizes from the Gulf of Aqaba, northern Red Sea. As a conservative estimate of mantle area, the planar area of naturally exposed clam mantles (cf. Griffiths and Klumpp, 1996) was calculated using Image J (version 1.33 for Windows) digital image analysis software, on scaled photographs of each clam. This was applied to obtain mantle areas and SL's, which were correlated as follows: $SL = a \times$ mantle surface^b; for *T. squamosa*, $n = 11$, $R^2 = 0.86$, $SL = 0.2688\ x^{2.0958}$ and *T. maxima*, $n = 18$, $SL = 0.2311\ x^{2.2388}$ $R^2 = 0.85$. Mantle area was 41–92 cm^2 for the incubated clams (Supplementary data, Table 2).

Calculations of metabolic needs

The percent contribution of zooxanthellar carbon to the clams (the hosts) daily requirements for respiration (CZAR) was calculated according to modifications of Trench et al. (1981) (Klumpp and Lucas 1994; Klumpp and Griffiths 1994; Fitt and Cook 2001), through the use and extrapolation of data obtained from the chamber incubations during the course of a day (clams reared in the outdoor tanks in the raceways, ~ 1 m depth).

$$\mathrm{CZAR} = \{[(P_{n,day} \times PQ^{-1} \times 0.375) + (R_{day} \times RQ \times 0.375) \times (0.95)] \times (\%T) \times 100\} / R_{24h} \times RQ \times 0.375 \times 0.95;$$

where $P_{n,\ day}$ is the net O_2-production within a day, R_{day} is the respiration during daylight, both quotients for respiration (RQ) and photosynthesis (PQ) are considered as 1 (Trench et al. 1981), 1 mg O_2 equals 0.375 mg C, $R_{24\ h}$ is the respiration over 24 h, the respiration due to the clam is assumed to be 95% of holobiont respiration (Trench et al. 1981; Klumpp and Griffiths 1994; Klumpp and Lucas 1994), and the translocation efficiency ($\%T$) is considered to be 95% (Muscatine 1990; Klumpp and Lucas 1994; Klumpp and Griffiths 1994).

$[(P_{n,day} \times PQ^{-1} \times 0.375) + (R_{day} \times RQ \times 0.375)$ $(0.95)] \times (\%T)$ is 'the daily translocated carbon production' of the zooxanthellae to their host clam, and $R_{24\ h} \times RQ \times 0.375 \times 0.95$ corresponds to the respiratory needs of the giant clam.

Zooxanthella density and pigment content

Mantle clips were taken and frozen for later analysis (−20°C); for zooxanthella density and high performance liquid chromatography (HPLC) pigment determination. The outer edge of the mantle was grasped with tweezers and a small piece (~ 0.8 cm^2) cut off with a scalpel. The number of clips was limited to one individual^{-1}, before and after shading, to minimize stress ($n = 4$ species^{-1} and treatment^{-1}, except *T. maxima* in shade: $n = 3$). Clip area was calculated using scaled photos (Image J 1.33). The

clips were later cut into small pieces, placed in an ice-cooled 250-ml vial and crushed with an 'Ultra-Torrax' at ~ 1,200 rpm. The solution was filtered through a 120-µm mesh screen (to separate tissue particles from the zooxanthella suspension), filled up to a constant volume, and zooxanthella density was determined using a Fuchs-Rosenthal haemocytometer.

Zooxanthella pigments were extracted using methanol according to Mobley and Gleason (2003), and subjected to HPLC according to Wright and Jeffrey (1997). HPLC analysis was conducted with a 'reverse phase HPLC 2996' from Waters and a '125 mm × 4 mm Vertex column packed with Spherisorb SC8 and 5-µmol particle size', at a reduced running time of only 24 min. Spectra were identified according to Jeffrey et al. (1997) and pigment contents quantified using Pigment Standards (DHI Water and Environment, The International Agency for ^{14}C Determination) and dilution series. Only chl *a* data are shown for this study. Unless otherwise stated, all values are given as mean ± SE.

Results

Fluorescence measurements

In spite of the exponential decrease of photosynthetically active radiation (PAR) with depth, both *T. squamosa* and *T. maxima* showed only a moderate linear increase in effective PSII quantum yield ($\Delta F/Fm'$) with depth (Fig. 1a, b), and a high scatter of within-depth variation, possibly due to light fluctuations, particularly in the shallow waters, and within- and between-individual variations (Fig. 1b).

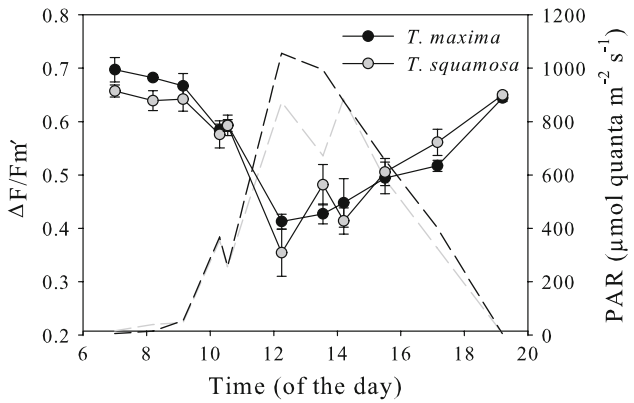

Fig. 2 *Tridacna maxima* and *T. squamosa*. Effective PSII quantum yield ($\Delta F/Fm'$) over 1 day. Clams were reared and measured in outdoor raceways (acclimatized to high light conditions at 1-m depth). *Black dashed line* shows light for *T. maxima* and gray dashed line light for *T. squamosa*, photosynthetically active radiation (*PAR*, µmol quanta m^{-2} s^{-1}) with daytime (hours), $n = 3$ species^{-1}, mean ± SE

Tridacna maxima and *T. squamosa* adapted to simulated water depths (shallow: high light, 3 m and deep: low light, 20 m) showed no significant differences in $\Delta F/Fm'$. This was true for both shallow (*T. maxima*: 0.50 ± 0.04 and *T. squamosa*: 0.48 ± 0.06, two sided *U*-test, $P = 0.77$) and deep conditions (~ 20 m: *T. maxima*: 0.65 ± 0.01 and *T. squamosa*: 0.69 ± 0.03, two sided *U*-test, $P = 0.2$) (Supplementary data, Fig. 2).

Both *T. maxima* and *T. squamosa* showed similar diel variations in $\Delta F/Fm'$ with highest values at daybreak ($\Delta F/Fm' \sim 0.7$, Fig. 2), a pronounced noontime depression ($\Delta F/Fm' < 0.4$, Fig. 2), followed by a gradual rise towards dusk, recovering to almost initial values at dark ($\Delta F/Fm' > 0.6$, Fig. 2).

Tridacna maxima and *T. squamosa* showed RLC with similar initial slopes and saturation light intensities but significantly different relative ETR saturation levels (Fig. 3), reaching an ETR_{max} of 314 ± 16 µmol e^- m^{-2} s^{-1} in *T. maxima* compared to only 250 ± 85 µmol e^- m^{-2} s^{-1} in *T. squamosa*. The saturation light intensity of ~ 2,500 µϖ mol quanta m^{-2} s^{-1} exceeded maximum ambient PAR levels (reef flat) by a factor of 2–3, and clams showed no signs of photoinhibition up to fourfold maximum photon fluxes during the short period of the RLC. *F*-values of the light curves steadily increased with PAR for both species, showing a higher overall performance for *T. squamosa*. The *F*-values at 2,343 µmol quanta m^{-2} s^{-1} were significantly higher compared to 2 µmol quanta m^{-2} s^{-1} (2,343 µmol quanta m^{-2} s^{-1} was used over 3,889 µmol quanta m^{-2} s^{-1}, the highest intensity, as more values were available; 2,343 µmol quanta m^{-2} s^{-1}: *T. maxima*, 283 ± 34 and *T.*

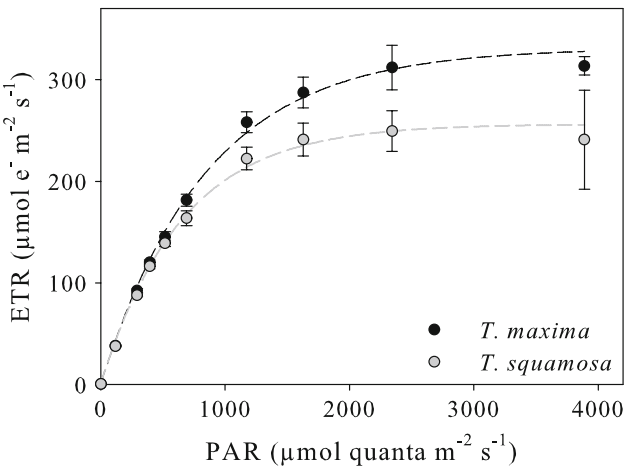

Fig. 3 *Tridacna maxima* and *T. squamosa*. Rapid light curves (*RLC*) of adult clams reared and measured in outdoor raceways (acclimatized to high light conditions at 1-m depth), electron transport rate (*ETR*, µmol e^- m^{-2} s^{-1}) with photosynthetically active radiation (PAR, µmol quanta m^{-2} s^{-1}), *T. maxima*: $R^2 = 0.95$, $y = 331.24\ (1 - e^{-0.0012\ (x)})$, *T. squamosa*: $R^2 = 0.90$, $y = 256.38\ (1 - e^{-0.0015\ (x)})$, $n = 3$ species^{-1}, mean ± SE

squamosa, 375 ± 116; 2 µmol quanta m^{-2} s^{-1}: *T. maxima*, 148 ± 19 and *T. squamosa*, 188 ± 52; two-sided, unpaired *t*-test, no homogeneity of variance; *T. maxima* $P = 0.008$, *T. squamosa* $P = 0.019$).

Chamber incubations

Under natural light conditions, *T. maxima* showed a barely significantly higher gross O_2 production than *T. squamosa* ($P_g = 0.198 \pm 0.077$ vs. 0.136 ± 0.015 µmol O_2 cm^{-2} min^{-1}, one sided *U*-test, $P = 0.057$). Clearer differences were found for shaded conditions lasting for 10 days ($P_g = 0.183 \pm 0.129$ vs. 0.060 ± 0.019 µmol O_2 cm^{-2} min^{-1}; *U*-test: one sided $P = 0.05$). Under low light, *T. maxima* reached 93 %, while *T. squamosa* attained only 44% of the initial values. The respiration rates (*R*) for both species were similar (*T. maxima*: $R = 0.044 \pm 0.014$ µmol O_2 cm^{-2} min^{-1} and *T. squamosa*: $R = 0.038 \pm 0.009$ µmol O_2 cm^{-2} min^{-1}, two sided *U*-test, $P = 1.0$, Fig. 4).

Diel net photosynthesis of *T. maxima* showed a bimodal distribution with a typical mid-day depression at 13.30 h, but overall higher performance than *T. squamosa.* Lacking the noon depression, *T. squamosa* reaches an O_2 production maximum around 13.00 h local summer time, i.e. when the sun was at its zenith (Fig. 5). Daily gross and net photosynthesis rates per day were extrapolated using the individual rates for a given time period and were higher for *T. maxima* than for *T. squamosa,* averaging 120.3 and 88.0 µmol O_2 cm^{-2} day^{-1} vs. 84.8 and 56.7 µmol O_2 cm^{-2} day^{-1}, respectively (two sided *U*-test, $P = 0.02$, Fig. 5).

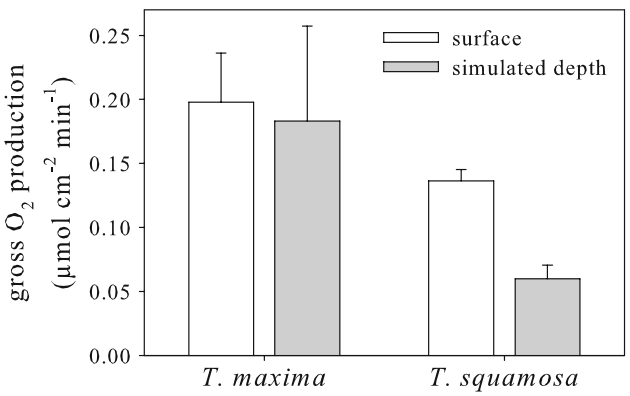

Fig. 4 *Tridacna maxima* and *T. squamosa*. Gross O_2 production (µmol cm^{-2} min^{-1}) of high and low light acclimatized clams (high light corresponds to 3-m depth and low light to shading conditions, simulating a depth of 20 m) incubated in their particular light conditions, $n = 4$ $species^{-1}$, except *T. maxima* in the shade = 3, mean ± SE

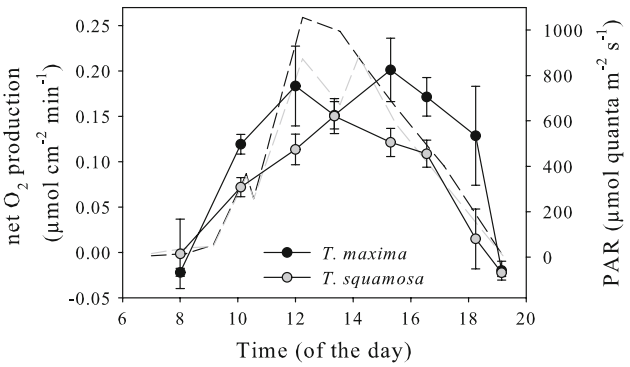

Fig. 5 *Tridacna maxima* and *T. squamosa*. Net O_2 production (µmol m^{-2} min^{-1}) of giant clams reared and measured in outdoor raceways (acclimatized to high light conditions at 1-m depth) over 1 day; *black dashed line* shows light for *T. maxima* and *gray dashed line* light for *T. squamosa*, photosynthetically active radiation (*PAR*, µmol quanta m^{-2} s^{-1}) with time of day (hours), $n = 3$ per species, mean ± SE

PAM-fluorometry in comparison to chamber incubations

Net O_2 production (P_n) was positively (Fig. 6a; *T. maxima*: $R^2 = 0.47$ and *T. squamosa*: $R^2 = 0.65$) and $\Delta F/Fm'$ negatively correlated with light (Fig. 6b; *T. maxima*: $R^2 = 0.95$ and *T. squamosa*: $R^2 = 0.93$). There was a good correlation between photosynthesis measured independently by pulse-amplitude fluorescence (ETR) and the chamber incubations (P_g) (Fig. 7; *T. maxima*: $R^2 = 0.53$ and *T. squamosa*: $R^2 = 0.61$).

Zooxanthella density and pigment content

Zooxanthellae occurred in densities of 15–19 × 10^6 cells cm^{-2} mantle area. Although we found lower values in shaded *T. squamosa,* and higher values in shaded *T. maxima*, these differences were not significant (*T. squamosa*: $14.5 \pm 2.4 \times 10^6$ cells cm^{-2} and *T. maxima*: $19.1 \pm 3.0 \times 10^6$ cells cm^{-2}; mean ± sd, $P = 0.096$; two-sided *t*-test, heterogeneity of variances, Table 1). The zooxanthella pigments showed significant increases under shading conditions within species (*T. maxima*, $P = 0.038$; T. *squamosa*, $P = 0.047$, two-sided *t*-test, heterogeneity of variances, Table 1), but no differences between species ($P = 0.20$, two-sided *t*-test, heterogeneity of variances).

Autotrophic input and metabolic needs

Considering photosynthetic activity lasting for the whole experiment (from dawn till dusk: 12.20 h), daily integrated gross (intP_g) and net O_2 production (intP_n) values averaged 120 and 88 µmol cm^{-2} day^{-1} for *T. maxima,* lower values

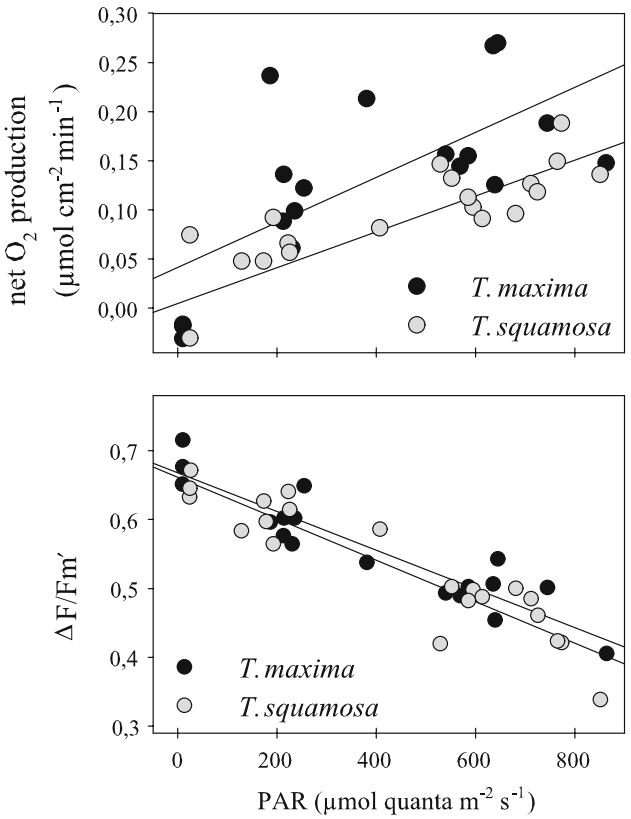

Fig. 6 *Tridacna maxima* and *T. squamosa*. Correlations of photosynthesis and light, each measuring point reflects one incubation per clam; **a** net O_2 production (µmol cm^{-2} min^{-1}) and photosynthetically active radiation (*PAR*, µmol quanta m^{-2} s^{-1}), *T. maxima*: $y = 0.0002$ $(x) + 0.0418$, $R^2 = 0.47$, *T. squamosa*: $y = 0.0002$ $(x) + 0.005$, $R^2 = 0.65$; **b** effective PSII quantum yield ($\Delta F/Fm'$) and photosynthetically active radiation (*PAR*, µmol quanta m^{-2} s^{-1}), *T. maxima*: $y = 0.6636$ $(x) - 0.0003$, $R^2 = 0.95$, *T. squamosa*: $y = 0.6636$ $(x) - 0.0003$, $R^2 = 0.93$

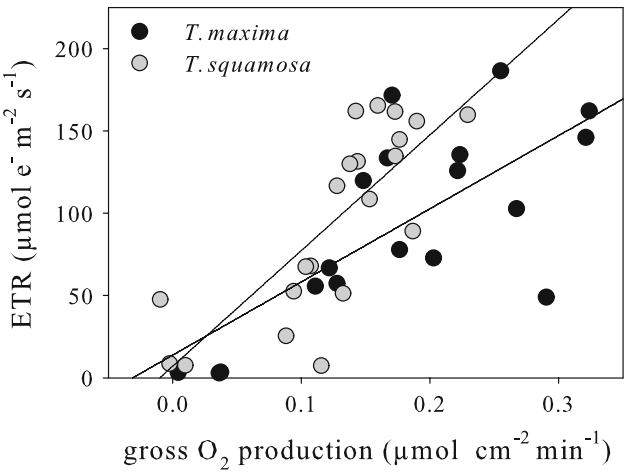

Fig. 7 *Tridacna squamosa* and *T. maxima*. Correlation of electron transport rate (*ETR*, µmol e^- m^{-2} s^{-1}) and gross O_2 production (µmol cm^{-2} min^{-1}), i.e. Diving PAM vs. chamber incubation, each measuring point reflects one incubation per clam, *T. maxima*: $y = 444.46$ $(x) + 13.89$; $R^2 = 0.53$, *T. squamosa*: $y = 702.77$ $(x) + 7.122$; $R^2 = 0.61$

being observed for *T. squamosa* (intP_g = 85 µmol cm^{-2} day^{-1}, intP_n = 57 µmol cm^{-2} day^{-1}). Therefore *T. squamosa* exhibited a much lower average O_2 production rate (0.077 µmol cm^{-2} min^{-1}) compared to *T. maxima* (0.12 µmol cm^{-2} min^{-1}). Conversion of the short-term respiration rates (*T. maxima*: 0.044 µmol cm^{-2} min^{-1} and *T. squamosa*: 0.038 µmol cm^{-2} min^{-1}) of the two species into a daily rate (24 h), amounts to 64 µmol cm^{-2} day^{-1} for *T. maxima* and 55 µmol cm^{-2} day^{-1} for *T. squamosa* respectively.

Assessment of metabolic needs was achieved through the calculation of the percent contribution of zooxanthellar carbon to the host's daily requirements for respiration (CZAR). *T. maxima* showed an overall enhanced productivity compared to *T. squamosa,* which is equivalent to 0.135 mg vs. 0.095 mg translocated C cm^{-2} day^{-1}. The respiratory carbon demand was similar for both species (0.073 mg vs. 0.063 mg C cm^{-2} day^{-1} for *T. maxima* and *T. squamosa*, respectively, Table 2). As a result, the translocated carbon exceeded the daily respiratory requirements by 86% (*T. maxima*) and 51% (*T. squamosa*), respectively (CZAR: 186 and 151%, Table 2).

Compensation depth

The CD is regarded as the depth where gross O_2 production equals the respiration demand for 24 h (i.e. gross O_2 production − respiration 24 h = 0). The O_2-values of the daylight performance (chamber incubations, Fig. 5) were used in computing CD. The gross O_2 production rate for each species at a given time (cm^{-2} min^{-1}) represents a certain part of the daily gross O_2 production.

Here we use particular gross O_2 rates (*T. maxima*: 0.228 µmol cm^{-2} min^{-1}, *T. squamosa*: 0.152 µmol cm^{-2} min^{-1}) at 11.00–12.00 h for further calculations (the same time when the later used light and depth correlation was obtained). These specific rates were regarded to correspond to the 186 and 151% CZAR (as mentioned above) and any changes in these rates are proportional to changes in CZAR.

At CD, overproduction should be 0% (100% CZAR), as metabolic needs are completely met by autotrophy. Accordingly, the selected rate was now reduced for denoting 100% CZAR and yielded values of 0.121 (µmol cm^{-2} min^{-1}) for *T. maxima* and 0.099 (µmol cm^{-2} min^{-1}) for *T. squamosa*. Further application of the correlation of gross O_2 production vs. PAR (*T. squamosa*: $y = 0.0002x + 0.0444$; $R^2 = 0.65$; *T. maxima*: $y = 0.0002x + 0.0866$; $R^2 = 0.39$), equals 274 and 170 PAR (µmol quanta m^{-2} s^{-1}; *T. maxima* and *T. squamosa*, respectively). These values in turn would correspond to a

Table 1 Zooxanthellae density and Chl *a* content

Species	Treatment	Zooxanthellae density (cm^{-2})	Chl *a* (μg per 10^6 zooxanthellae)
T. maxima	Light	$18.8 \times 10^6 \pm 6.2 \times 10^6$	2.52 ± 0.37
T. maxima	Shade	$19.1 \times 10^6 \pm 3.0 \times 10^6$	3.33 ± 0.37
T. squamosa	Light	$16.6 \times 10^6 \pm 2.5 \times 10^6$	2.73 ± 0.61
T. squamosa	Shade	$14.5 \times 10^6 \pm 2.5 \times 10^6$	4.08 ± 0.90

Tridacna maxima and *T. squamosa*: zooxanthellae density per cm^2 mantle area and Chl *a* contents per zooxanthellae cells under high light conditions and after adaptation to shading for 10 days (simulating 20 m depth) conditions ($n = 4$, except *T. maxima* in shade, $n = 3$; mean ± standard deviation)

Table 2 The percent contribution of algal carbon to the host's daily requirements for respiration (CZAR)

Metabolic aspects (mg C day^{-1} cm^{-2})	*T. maxima*	*T. squamosa*
CZAR (%)	186	151
Translocated production by zooxanthellae	1.35	0.951
Respiratory demand of host	0.0726	0.0632
$P_{n,day}$	2.81	1.81
R_{day}	1.04	0.90
$R_{24\ h}$	2.04	1.77

Tridacna maxima and *T. squamosa* reared at the outdoor raceways (acclimatized to high light conditions in 1-m depth): translocated production by zooxanthellae: daily translocated carbon production of zooxanthellae to their host; respiratory demand of host: daily needs of carbon for the respiratory demand of the host

$P_{n,day}$ net O_2-production of zooxanthellae within a day, R_{day} respiration during daylight of the host, $R_{24\ h}$ respiration during 24 h of the host

CD of 16 m for *T. maxima* and 9 m for *T. squamosa* (using light vs. PAR correlation, obtained at 11.00–12.00 h, Supplementary data, Fig. 1, $PAR = 188.57\ e^{-0.087x}$, $R^2 = 0.9571$). Even though these values are estimates, they suggest a much deeper CD for *T. maxima*.

Discussion

Differences in the vertical distribution of the two species of giant clams can only partly be attributed to differences in their photosynthetic performance, suggesting there are also differences in feeding strategies. In line with our original hypothesis, shallow-dwelling *T. maxima* was found to be a high-light specialist, tolerating extreme PAR intensities, and showed no photoinhibition well beyond maximum natural levels of illumination on the reef flat. Interestingly, it can also maintain high productivity under reduced light levels as illustrated by our shading experiments. The estimated CD agrees with the maximum vertical distribution of *T. maxima*. Thus, *T. maxima* is capable of flexible photoadaptation and its vertical range appears to be limited by light, leading to the conclusion that *T. maxima* is functionally autotrophic. Further support for this was found in the Pacific Islands, where very clear oceanic water allows for a much deeper CD, and *T. maxima* is indeed found down to 32 m (e.g. Cook Island, Sims and Howard 1988); likely reflecting the greatest CD for this species.

Surprisingly, the deep-dwelling *T. squamosa* (down to 42 m) is not a low-light specialist. This species exhibits a lower productivity in general, even under high light conditions, and a reduced ability to adapt to low light conditions. This lower photosynthetic potential is further confirmed by an estimated lower CD. *T. squamosa* must rely on an additional heterotrophic feeding strategy, such as filter feeding, to satisfy its metabolic needs within its range of distribution, especially in deeper waters, and therefore must be a true mixotrophic species.

Moreover, the CD estimated for *T. squamosa* in the present study will be shallower when light intensity decreases, i.e. during winter or on cloudy days, and heterotrophic nutrient sources will become more and more crucial. Even though Mangum and Johansen (1982) doubted the filtering capability of *T. squamosa*, a later study by Klumpp and Griffiths (1994) showed clearance rates in *T. squamosa* comparable with those of *T. crocea* and *H. hippopus*.

In their study on *T. derasa* and *T. tevoroa*, Klumpp and Lucas (1994), related the CDs of the two species to their maximum natural depth occurrence, filter feeding remaining constant independent of light levels. Most studies on giant clams support the important role of autotrophy in their nutrition, especially in the juvenile stages, and high-light filter-feeding as a secondary food source (Fisher et al. 1985; Klumpp and Griffiths 1994).

Metabolic features were only evaluated for autotrophic input and respiration in the present study, not the potential heterotrophic input for *T. squamosa*. *T. maxima* may have an advantage over *T. squamosa* in shallow waters, displaying similar respiration rates but higher autotrophy. Additionally, the zooxanthellae of *T. maxima* seem to satisfy their nutrient requirements (N and P) mainly through their host's excretion products; they are not limited by nutrients and therefore not sensitive to nutrient enrichment (Ambariyanto and Hoegh-Guldberg 1997).

Energy, invested into growth, requires on average (except for *T. gigas*) 20–40% of the demand of carbon used for respiration (e.g. *T. squamosa*: Klumpp and Griffiths 1994, *T. tevoroa* and *T. derasa*: Klumpp and Lucas 1994). The relative contribution of photosynthesis compared to heterotrophy, increases with SL, with maximum values for *T. gigas*, whereas *T. squamosa* can be found in the mid-range (Klumpp et al. 1992; Klumpp and Griffiths 1994; Klumpp and Lucas 1994). *T. maxima* was not included in any of these studies but may cover an equivalent range. Respiration and growth rates decrease concomitantly with increasing SL (Fisher et al. 1985; Klumpp et al. 1992; Klumpp and Lucas 1994). As the incubated clams were not fully grown adults (Beckvar 1981; Manu and Sone 1995) and there will be a higher CZAR with increasing size (while carbon demand declines proportionally), we may have underestimated CZAR in our study. This may also affect their CD, inferring a deeper CD for larger individuals; as indicated by Roa-Quiaoit and Richter (in review) who found a size-frequency shift towards larger specimens of *T. squamosa* in deeper waters. One possible explanation is that the required heterotrophic input, i.e. the filter feeding, may not be efficient or profitable enough for small individuals, so only a few survive each year.

Klumpp and Griffiths (1994) calculated a CZAR of $\sim$ 255% for *T. squamosa*, thus $\sim$ 169% higher than found by this study. The deviating CZAR may be due to different light conditions or measuring methods. Moreover, Klumpp and Griffiths (1994) measured respiration rates and oxygen production simultaneously. For the present study, respiration was only measured over short time incubation and it was assumed that respiration would be stable throughout the day. This is supported by constant respiration rates measured on *T. tevoroa* and *T. derasa* (Klumpp and Lucas 1994) and on *T. gigas* (Klumpp et al. 1992), independent of light history and time of day.

Considering *T. maxima*'s maintenance of 93% gross oxygen production under shading conditions compared to initial values, presumably increasing chl *a* content per cell yields a better adaptation to low light levels. There are different reactions for the entire holobiont to adapt to low light conditions. Titlyanov et al. (2001) found that *Stylophora pistillata* adapted to low light conditions (30% 'surface irradiance', matching shading conditions of the present study), by increasing the zooxanthella density polyp^{-1}. Zooxanthellae extracted during a reduction of light from 250 to 40 (PAR, µmol quanta m^{-2} s^{-1}) of the 'up-side-down-Jellyfish' *Cassiopeia xamachana*, the stony coral *Montipora verrucosa*, and the zoanthid *Zoanthus sociatus* reacted likewise with an increase of chl *a* content per cell (Iglesias-Prieto and Trench 1994). Zooxanthella density cm^{-2} mantle area was highly variable in the two species of giant clams, as the tubular system containing the zooxanthellae distributes them unequally over the mantle (Norton et al. 1992).

Although giant clams exhibited no visible sign of photoinhibition, (no decrease of ETR was reached after the saturation plateau), presumably reversible photoinhibition did occur. Such an assumption is based on significant increases in *F*-values at 2,342 PAR compared to *F*-values under natural light conditions. This may be due to reversible photoinhibition (in contrast to photodamage), which in turn is due to an increase of non photochemical-quenching, the release of an excess of light energy as heat and therefore, a down regulation of PS II, which is also found in corals (Ralph et al. 1999; Gorbunov et al. 2001; Lesser and Gorbunov 2001). Photoinhibition during the RLC may remain undetected as the duration of the RLC (1–2 min) is much faster than the time needed for the xanthophyll-cycle and other physical reactions to start (5–30 min, Ralph et al. 1999).

Furthermore, symbiotic clams obtain 'mycosporine-like amino acids' (MAAs) for UV protection (*T. crocea, T. derasa, H. hippopus*, *Colculum cardissa*, and *Fragum unedo* Ishikura et al. 1997) from their food. These MAAs are also found in corals and their content increases with decreasing depth (Shick et al. 1995; Lesser 2000). It should also be considered that in the mantle of the Tridacnidae, the so-called 'Iridiophores' may reflect (Griffiths et al. 1992), and the opalescent pigments may filter, parts of the incoming light (Ralph et al. 1999). These two phenomena could result in an overestimation of the photosynthetic performance by fluorescence measurements. This would not have occurred in the investigations of photosynthesis through chamber incubations, which in turn showed a consistent correlation with oxygen production.

Overall, the Diving PAM appears to be a practical method for investigating the photosynthetic performance of giant clams because it is easy to use in situ. The giant clams examined in this study seem to adapt well to changes in light availability, responding with an alteration in their photosynthetic efficiency. Both species tolerated high light intensities reaching very high saturation values (> 2,500 PAR, µmol quanta m^{-2} s^{-1}). This is in agreement with Ralph et al. (1999) who conducted RLC on one specimen of *T. maxima* up to a light intensity of 2,000 PAR, which revealed no saturation within this range. Beer et al. (1998) found saturation intensities of 1,500–2,000 (PAR, µmol quanta m^{-2} s^{-1}) for the corals *Favia favus* and *Platygyra lamellina* in shallow water (3–4 m). Adaptation to varying light availability has also been detected through RLC on *Acropora aspera* living at different depths (Ralph et al. 1999).

Transplantation experiments of adult Tridacnidae suggest a relatively short adaptation time of a few days to different depths considering $\Delta F/Fm'$ measurements (own

unpublished data). Warner et al. (2002) recorded $\Delta F/Fm'$ of corals (*Montastrea annularis*, *Montastrea faveolata*, *Montastrea franksi*) in the Bahamas for 2–5 years, over seasonal variations of light availability. Highest values occurred in winter and early spring and lowest in mid- to late summer, and the difference between seasons was as much as 15%. As the measurements in this study were done in spring to early summer, they may exhibit an intermediate $\Delta F/Fm'$, compared with higher values in winter and lower in summer, so the maximum and minimum range for a certain depth at a given time may not have been achieved.

Acknowledgements This study was funded by the German Ministry for Education and research (grant no. 03F0356A). Thanks are due to the scientific and technical staff of the MSS, in particular to Mohammed Rasheed, Yousef Ahmed and Abdullah Al-Momany (diving supervision) for support. Thanks to Matthias Birkicht and Stefani Bröhl for technical advice and logistics at the ZMT. Special thanks to Ralph Tollrian for supporting this study, especially the part in Dahab. Thanks to the MPI, notably Dirk deBeer and Raphaela Schoon for HPLC access and assistance.

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